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Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective

J. A. Estes[1,*], D. F. Doak[2], A. M. Springer[3] and T. M. Williams[1]

[1]*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060, USA*
[2]*Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82072, USA*
[3]*Institute of Marine Science, University of Alaska, Fairbanks, AK 99775, USA*

Populations of sea otters, seals and sea lions have collapsed across much of southwest Alaska over the past several decades. The sea otter decline set off a trophic cascade in which the coastal marine ecosystem underwent a phase shift from kelp forests to deforested sea urchin barrens. This interaction in turn affected the distribution, abundance and productivity of numerous other species. Ecological consequences of the pinniped declines are largely unknown. Increased predation by transient (marine mammal-eating) killer whales probably caused the sea otter declines and may have caused the pinniped declines as well. Springer *et al.* proposed that killer whales, which purportedly fed extensively on great whales, expanded their diets to include a higher percentage of sea otters and pinnipeds following a sharp reduction in great whale numbers from post World War II industrial whaling. Critics of this hypothesis claim that great whales are not now and probably never were an important nutritional resource for killer whales. We used demographic/energetic analyses to evaluate whether or not a predator–prey system involving killer whales and the smaller marine mammals would be sustainable without some nutritional contribution from the great whales. Our results indicate that while such a system is possible, it could only exist under a narrow range of extreme conditions and is therefore highly unlikely.

Keywords: killer whale; sea otter; pinniped; Bering Sea/North Pacific; trophic cascade; indirect effects

1. INTRODUCTION

Because all heterotrophs must eat other living things to survive and reproduce, consumer–prey interactions are among the biosphere's most fundamental processes. In their simplest conceptualization, food webs define the trophic linkages among species. However, a deeper look reveals nuance and complexity (Paine 1988). Interspecies trophic connectivity can be direct or indirect, bottom-up or top-down, weak or strong and invariant or context dependent. Thus, it is not surprising that a variety of approaches have been taken in an effort to understand food-web dynamics. These range from theoretical to empirical, from descriptive to experimental and from holistic (all species) to more selectively focused (e.g. on autotrophs, apex predators, parasites) considerations of the drivers of dynamic processes.

Within this diverse field, our primary interest is on how large apex predators influence food-web dynamics. Once components of most natural ecosystems, large predators today are absolutely or functionally extinct over much of the global land and seascape. There is good reason to suspect that these species are or were important drivers of food-web dynamics. Many

have elevated metabolic rates, which, when combined with their high trophic status, create high *per capita* nutritional requirements. Furthermore, there is growing evidence for strong consumer-mediated effects of apex predators in diverse ecosystems (Pace *et al.* 1999).

Here, we focus on the food-web dynamics of nearshore marine ecosystems in southwest Alaska, defined as the western Gulf of Alaska, Aleutian Islands and eastern Bering Sea. This region, until recently, was literally festooned with a diversity of large marine mammal predators, including a dozen or so species of small cetaceans, three species of pinnipeds, sea otters (*Enhydra lutris*) and over 15 species of great whales. During the 1960s and 1970s, harbour seal (*Phoca vitulina*), Steller sea lion (*Eumetopias jubatus*), northern fur seal (*Callhorinus ursinus*) and sea otter populations declined precipitously throughout the area (National Research Council 1996, 2003). Before this, human exploitation had dramatically reduced whale populations in the same area. We will consider the causes and consequences of these multiple declines and especially the role of another marine mammal, the killer whale, in linking species and driving the food-web dynamics. The system has advantages and disadvantages for understanding food-web dynamics. The area is remote and the key species live on or under the high seas, conditions that are less than ideal for doing research. On the other hand, the declines are of substantial concern to conservation and management;

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they constitute a large-scale perturbation of mesopredators, which occurred while we were working in the area, and time-series data are available for various components of the system, from which the causes and consequences of the megafaunal collapse can be inferred.

Although we are especially concerned with food-web interactions involving marine mammals in the North Pacific, our work may shed light on additional systems and larger issues. Other marine and terrestrial communities have or are undergoing similarly linked, multi-species declines or recoveries (not least of which were Pleistocene extinctions on several continents), and in all cases we know even less about the chains of causation. Therefore, we are interested in using the Alaskan marine system both for addressing questions of causality and for testing the strength of possible ecosystem linkages in the face of human perturbations.

2. MEGAFAUNAL COLLAPSE IN THE NORTH PACIFIC

Fur seal and sea otter populations were greatly reduced by the Pacific maritime fur trade of the eighteenth and nineteenth centuries. Following protection early in the twentieth century, both species made strong recoveries. The history of sea lion and harbour seal populations in southwest Alaska is more poorly known, although the remoteness of this area and the species' lack of commercial value probably acted in combination to prevent population declines from commercial exploitation or fisheries mitigation. Except for the extinct Steller sea cow (*Hydrodamalis gigas*), all or most of the native marine mammals are thought to have occurred at high natural abundances through World War II. Post World War II, industrial whaling dramatically depleted the great whales in the decades that followed the war, ending in 1976 with a complete moratorium on commercial whaling (figure 1*a*). Harbour seal populations began to decline in the late 1960s or early 1970s, followed by Steller sea lions and then sea otters. The mid-points of these declines occurred sequentially, at about decadal intervals (figure 1*b*). By contrast, the declines are spatially coincident, ranging from about the Kodiak archipelago in the east to the western Aleutian archipelago in the west (National Research Council 2003).

3. CONSEQUENCES OF THE MEGAFAUNAL COLLAPSE

Due primarily to the long history of research on the sea otter's role in food-web and ecosystem dynamics, some of the consequences of this species' recent population collapse in southwest Alaska are well known. Most of this understanding comes from the contrasts among islands with and without sea otters, and from the time-series measurements at islands where otter numbers have changed (Estes & Duggins 1995; Estes *et al.* 2004). Sea otters consume sea urchins, and sea urchins consume kelp and other fleshy macroalgae. By preying on sea urchins, sea otters thus initiate a trophic cascade in which kelp is enhanced. Systems lacking sea otters, by contrast, are typically deforested by sea urchin grazing. The dynamics of the plant–herbivore interaction are complex and highly nonlinear, owing
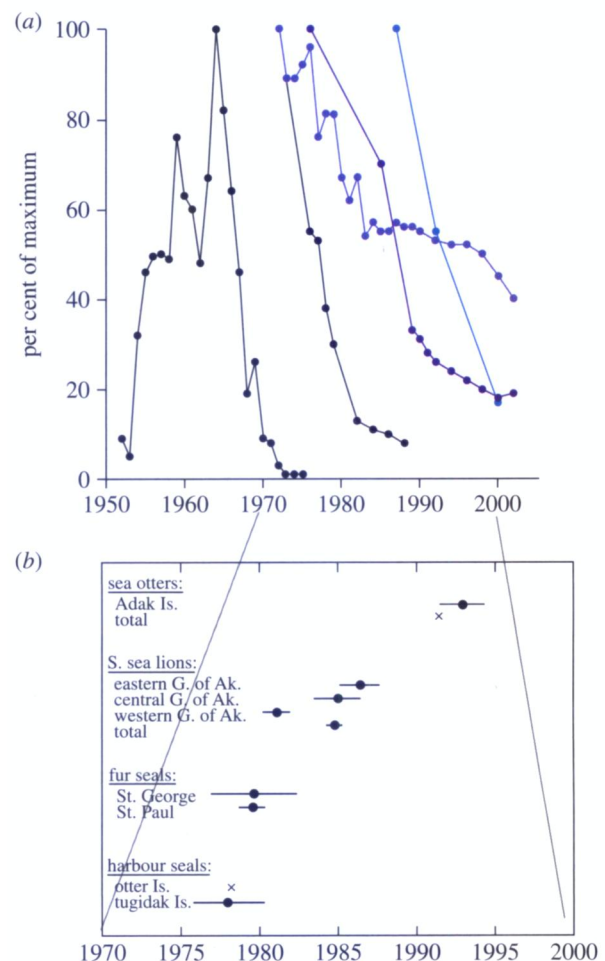

Figure 1. (*a*) Time series (from left to right) of population change of great whales, harbour seals, northern fur seals, Steller sea lions and sea otters in the North Pacific Ocean and southern Bering Sea (from Springer *et al.* 2003). (*b*) Data are the best estimates (circles) and 95% CIs from the best available survey data (details of data sources and model fitting are in Springer *et al.* 2008).

to the behavioural shifts by sea urchins when kelps are either rare or abundant (Harrold & Reed 1985; Konar 2000), and the kelp's ability, once established in dense stands, to deter sea urchin attack (Konar & Estes 2003). The system, as a result, tends to exist in one of two phase states—well-developed kelp forests or extensively overgrazed sea urchin barrens (Steneck *et al.* 2002). Intermediate community configurations are unstable and highly transitory.

Markedly different food-web dynamics are associated with these two ecosystem phase states, due largely to the presence or absence of kelp and the resulting effects of kelp in enhancing production, increasing three-dimensional habitat structure, and attenuating water motion from waves and currents. These effects in turn influence the physiology, behaviour and demography of myriad and diverse associated species. For instance, when sea otters are lost from a system, the growth rates of filter feeding barnacles and mussels decline two- to threefold (Duggins *et al.* 1989); rock greenling (*Hexagrammos lagocephalus*, a common kelp forest fish) population density declines approximately 10-fold (Reisewitz *et al.* 2005); the diet of Glaucous-winged gulls (*Larus glaucescens*) shifts from fish to
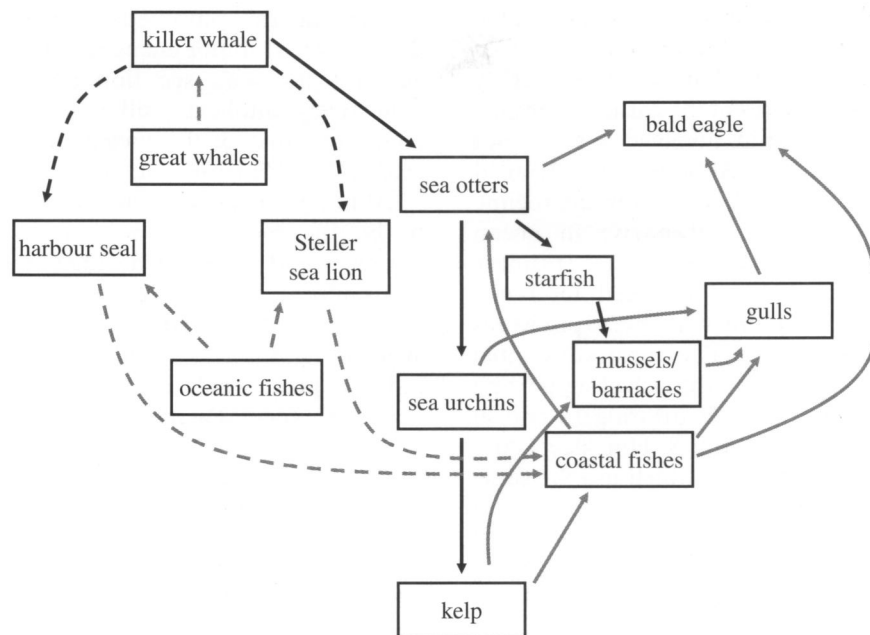
Figure 2. Food-web relationships among selected species in the North Pacific Ocean and southern Bering Sea. The arrows represent linkages for which there are known (solid lines) or suspected (dashed lines) dynamic interactions. Black arrows represent top-down forcing and the grey arrows represent bottom-up forcing. Strong dynamic responses are known for food-web pathways that connect at least eight species (e.g. great whales → killer whales → sea otters → sea urchins → kelp → coastal fishes → gulls → bald eagles). See text for explanations.

invertebrates (Irons *et al.* 1986); the diet of bald eagles (*Haliaetus leucocephalus*) changes from approximately equal parts of fishes, birds and mammals to domination by marine birds (Anthony *et al.* 2008); common eider populations increase (D. B. Irons, G. V. Byrd & J. A. Estes 1976–2008, unpublished data); the biomass density of subtidal starfish populations declines one to two orders of magnitude; and the reduced starfish abundance, which are important predators in their own right (Duggins 1983; Paine *et al.* 1985), reduces the intensity of predation on various invertebrate prey (figure 2).

In contrast to sea otters and kelp forests, almost nothing is known about the consequences of the pinniped declines. This is due in part to the fact that the neritic systems in which pinnipeds feed are more difficult to observe and study, and in part to the strongly held bottom-up perspective by many researchers working on pinnipeds in this region (i.e. Trites & Donnelly 2003; Trites *et al.* 2007a,b; Holmes *et al.* 2008). Nonetheless, strong top-down forcing effects by pinnipeds in southwest Alaska are likely. Sea lions and harbour seals are substantially larger than sea otters, their abundances and metabolic rates are comparable when scaled to body size (Williams *et al.* 2001) and most of their foraging occurs close to shore. It is worth noting that Atka mackerel (*Pleurogrammus monopterygius*), a primary prey of sea lions in the central and western Aleutians (Merrick *et al.* 1997), were rarely seen in shallow nearshore waters before the pinniped declines but are now very common, sometimes occurring in vast schools that extend from the water's surface to near the seafloor (J.A. Estes 1995–2008, personal observation). Furthermore, pinnipeds are known or suspected to initiate top-down food-web interactions in other systems (Power & Gregoire 1978; Boveng *et al.* 1998).

As with the pinnipeds, and for similar reasons, the ecological consequences of the great whale depletions in the North Pacific are difficult to assess (Estes *et al.* 2006). However, a hint of the likely impacts can be seen from the analyses by Croll *et al.* (2006) who estimated that some 65 per cent of the net primary production in the North Pacific Ocean was consumed by great whales prior to their industrial-scale exploitation. Through the direct and indirect effects of altered consumption, as well as disturbance effects (Highsmith *et al.* 2006), the marked decreases in most great whale stocks in our area of interest are almost certain to have had ecosystem-wide effects.

4. CAUSES OF FAUNAL COLLAPSES IN THE NORTH PACIFIC REGION

The underlying reasons for the sequential collapses of pinniped and otter populations in this area have been a matter of substantial interest, around which there is no small amount of controversy. The various hypotheses advanced to explain the collapses involve two fundamentally different processes—bottom-up and top-down forcing (National Research Council 2003). In one way or another, the bottom-up forcing hypotheses posit the underlying mechanism to be nutritional limitation. Competition with fisheries and ocean regime shifts are the two most credible explanations. Reasons for embracing these hypotheses, if not compelling (National Research Council 2003), are understandable. The scientific culture in oceanography is primarily one of bottom-up forcing, so a search for explanations within that framework is to be expected. Furthermore, there are reasons to suspect competition with fisheries, especially given that fisheries in the southeastern Bering Sea and Bristol Bay land several million tons annually. A more fragile

logic surrounds the ecological effects of oceanographic regime shifts, one of which occurred in the late 1970s (Frances & Hare 1994; Hare & Mantua 2000), roughly coincident with the early phases of the earliest pinniped population declines. This shift involved a small but abrupt temperature increase. Although the detailed mechanisms remain unspecified, implicit in the regime shift hypothesis is the idea that a rise in ocean temperature, or other physical changes, reduced primary and secondary productivities or changed food-web structure in a manner that was unfavourable to piscivores (e.g. Anderson & Piatt 1999). The most substantial problem with bottom-up forcing is the lack of supporting evidence. Prey biomass did not decline during the critical period of pinniped collapses (Fritz & Hinckley 2005; Brown 2007); seabird populations, which use the same prey in the same ecosystem, have not experienced similar, broad declines (Dragoo *et al.* 2007); and observed changes in the behaviour and physiology of pinnipeds are largely inconsistent with nutritional limitation (National Research Council 2003).

Top-down forcing hypotheses hold that the marine mammal population declines were driven by their consumers. Three specific causes have been proposed: disease pandemics; by-catch in fisheries or other forms of direct human take; and mortality from large predators such as sharks or transient killer whales, the latter representing the form of killer whales that are marine mammal specialists (as opposed to fish–eating ecotypes) and are thus the apex predator of the northern North Pacific (National Research Council 2003). There is no credible evidence for a pandemic in any of the species and populations that have declined (National Research Council 2003; Burek *et al.* 2005; Southwest Alaska Sea Otter Recovery Plan, US Fish and Wildlife Service, preliminary draft). Both purposeful shooting and incidental take in fishing gear killed numerous Steller sea lions (National Research Council 2003; NMFS 2008), but these losses did not occur over much of the region of the declines. Increases in salmon shark (*Lamna ditropis*) and sleeper shark (*Somniosus pacificus*) populations have led to suspicions that shark predation caused the pinniped declines, but shark populations do not appear to have increased throughout the geographical range of these declines and to date there is no evidence that local shark species attack and kill living marine mammals (National Research Council 2003).

In contrast to the negative evidence discussed above, there is reasonably compelling evidence that killer whales were responsible for at least the sea otter declines: this includes increased sighting and attack rates of killer whales on sea otters; sea otter population stability in refuge habitats from killer whale predation; the absence of stranded otter carcasses during the period of the population decline; and an analysis showing that the observed number of attacks by killer whales on sea otters was similar to that expected if increased killer whale predation were the sole cause of the decline (Estes *et al.* 1998). Although evidence of similar breadth and quality is lacking for the seals and sea lions (due to a lack of field study), the facts that killer whales commonly prey on these species, that the spatial extent and rates of population decline were

similar for the pinnipeds and sea otters, and the discovery that minor changes in killer whale diet could account for seal, sea lion and sea otter declines collectively implicate killer whale predation as the common cause of the megafaunal collapse (Springer *et al.* 2003; Williams *et al.* 2004).

Although increased killer whale predation appears to be the most parsimonious explanation for the sea otter and pinniped declines, the question of why this happened is less certain. Springer *et al.* (2003) proposed that the causal mechanism was post World War II industrial whaling, which substantially reduced great whale biomass in the southern Bering Sea and North Pacific Ocean (Pfister & DeMaster 2006). The idea is that human impacts on a key prey guild had shifted food-web structure via changing diet sources for a high-level predator. Briefly, Springer *et al.* suggested that great whales were a significant nutritional resource to transient killer whales. Industrial whaling, which targeted the great whales but left killer whales effectively unexploited, reduced the *per capita* availability of great whale fodder for transient killer whales. Springer *et al.* further proposed that, in response to this reduction, killer whales expanded their diets to include more of the smaller marine mammal species, which increased seal, sea lion and sea otter mortality to unsustainable levels, thus driving these prey populations sharply downwards. The sequential nature of the harbour seal, Steller sea lion and sea otter population collapses (figure 1) was taken by Springer *et al.* as further evidence for a consumer-mediated decline, the logic being that dietary expansion by transient killer whales is consistent with the basic tenants of optimal foraging (Krebs & Davies 1997) as one prey species after another was progressively depleted (Mangel & Wolf 2006) according to caloric value (Williams *et al.* 2004).

5. EVALUATING SPRINGER *ET AL.* WITH DATA AND LOGIC

The Springer *et al.* hypothesis was challenged on various fronts (Trites *et al.* 2007a; Wade *et al.* 2007), and these challenges were subsequently countered (Springer *et al.* 2008). The most controversial part of the debate is over the strength of the food-web linkage between killer whales and great whales. Mizroch & Rice (2006) argued that trophic interactions between killer whales and great whales are relatively unimportant, given that attacks are rarely seen and that large whale remains are rare or absent in the stomachs of harvested killer whales. Springer *et al.* (2008) countered by pointing out that any such remains, lacking hard parts, would have been difficult to identify and that the stomachs contained almost no remains of any marine mammals, not just large whales. Springer *et al.* (2008) further noted that many living whales bear scars from killer whale attacks, and that observed attacks by killer whales on coastal species such as grey whales are commonplace. Furthermore, the expected number of observed attacks on other great whale species in the pelagic realm is exceeding low, even if they were common and important (Doak *et al.* 2006). And

finally, most large whales display highly choreographed and stereotypic behaviours that are most easily explained as defences to killer whale predation.

The fact that such large numbers of whales bear scars from killer whale attacks would seem to constitute reasonably compelling evidence that attacks by killer whales on large whales are common and important events. However, Mehta *et al.* (2007) countered this point by reporting that the scaring in humpbacks occurs at lower latitudes, from which they reasoned that large whales are not important prey of killer whales in high-latitude oceans and thus concluded that a key assumption underlying the Springer *et al.* hypothesis was invalid. We question Mehta *et al.*'s logic on several grounds. First, since both transient killer whales and great whales are most abundant in high-latitude seas, the argument is internally inconsistent. Second, scars are not proxies for the frequency of attacks; they are records of the animals that escaped. Third, numerous attacks by killer whales on various species of great whales have been documented in high-latitude oceans as, for example, the carnage that occurs near Unimak Pass in the eastern Aleutian archipelago as killer whales lay in ambush for grey whales during their northern and southern migrations, and the growing frequency of fatal attacks on humpbacks in Alaska in recent years (Springer *et al.* 2008). Finally, the distribution and abundance of great whales is quite different today than it was before industrial whaling. The data presented by Mehta *et al.* (2007) may mean something, but exactly what is unclear.

To our minds, the biggest hole in past efforts to test the likelihood of the Springer *et al.* hypothesis has been the lack of analysis of the full range of possible food resources that are available to transient killer whales, and how much the past and current energetic needs of these predators could be filled without there being substantial consumption of great whales. In the following section, we attempt to tackle this analysis, asking: are or were transient killer whale populations sustainable on a marine mammal diet lacking large whales?

6. IMPORTANCE OF ALTERNATIVE PREY RESOURCES FOR KILLER WHALES

Insight into the relative importance of different killer whale food resources can be obtained through energetic/demographic bookkeeping; knowing only the abundance, field metabolic rate and consumption efficiency of the predator; and the abundance, caloric value and the life history (i.e. age-specific fertility, mortality and growth) of the prey (figure 3). Employing simple demographic modelling approaches (Caswell 2001; Morris & Doak 2002) and energetic-needs calculations, this information can be used to conduct feasibility analyses for specific dietary scenarios, thus moving debate from poorly supported conjectures over whether or not some consequence of a food-web interaction occurred to assessments of whether or not it could have occurred and if so how easily. 'No' answers are especially powerful because they permit the rejection of hypotheses (figure 4).

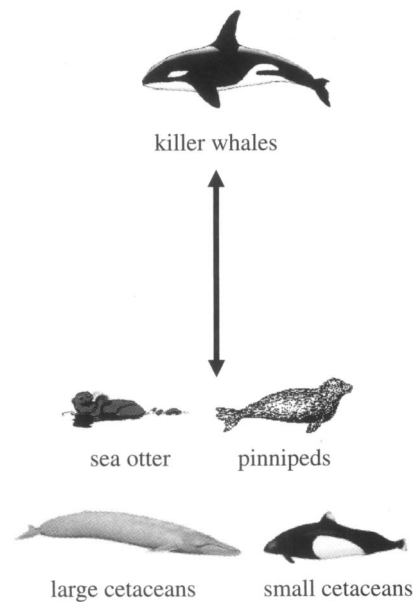We first used this approach to show that killer whale predation could have caused the excess deaths needed

Figure 3. Species and measurements used in the feasibility analyses based on their demography and energetics. (Predator: killer whales (abundance, field metabolic rate, consumption efficiency); prey: sea otter; pinnipeds; large cetaceans; small cetaceans (life history, caloric value, abundance)).
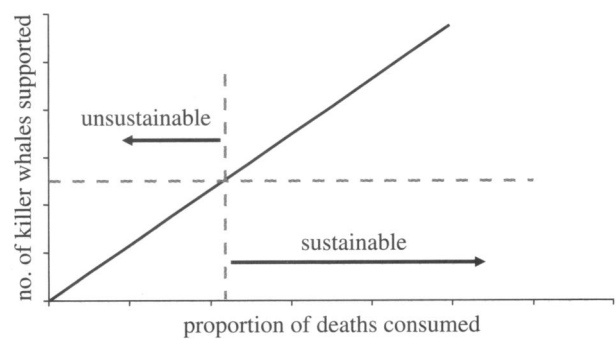

Figure 4. Graphical representation of sustainability analyses. The horizontal axis depicts the proportion of the maximum sustainable mortality that would have to be consumed by transient killer whales to support the number of animals depicted on the vertical axis.

to drive the sea otter and pinniped declines with only small changes in dietary composition or the number of predators (Estes *et al.* 1998; Williams *et al.* 2004). Because this is a 'yes' answer, the process is open to alternative interpretations.

We have also used demographic/energetic modelling to ask whether changes in great whale populations due to human exploitation could have resulted in substantial differences in killer whale food resources in the North Pacific (Doak *et al.* 2006). Here, we expand this approach to ask what kinds of transient killer whale dietary scenarios are consistent with sustainable prey populations, and in particular whether the current transient killer whale predator–prey system is sustainable without the predation/consumption of large whales. In addition to information on gross caloric value, life history and population abundance identified above, the essential variables in these calculations are (i) the species and life stages of prey that are attacked and eaten by killer whales, (ii) the fraction of prey deaths that result from predation, (iii) the prey tissue types that are eaten,
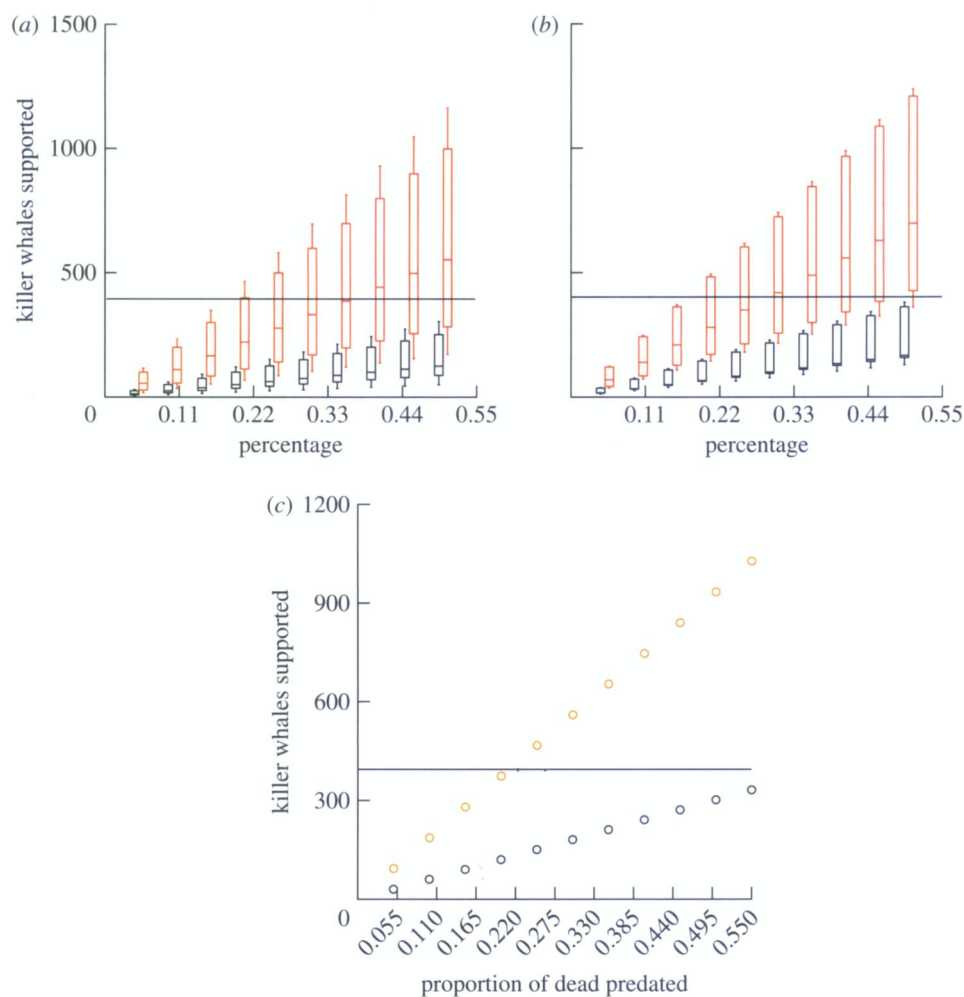
Figure 5. Numbers of killer whales that could be supported by historical and current populations of great whales or small marine mammals. Each set of boxplots or points show distributions of estimated killer whale numbers currently (grey) or historically (red) as functions of the fraction of animals dying that are predated: (*a*) only young great whales and minke whales consumed, (*b*) young, minkes, and tongues and blubber of adults consumed, (*c*) small marine mammals (seals and porpoises) consumed. Horizontal lines at 400 indicate the minimum number of transient killer whales that presently occur in the system. For great whales, boxplots are shown to indicate the range of predictions over the different parameter values governing consumption and population regulation (see Doak *et al.* (2006) for further details); for small marine mammals, only averages of the two scenarios for historic population regulation are shown.

Table 1. Current and historical estimates of small marine mammal abundance in the North Pacific Ocean and southern Bering Sea. (Data from Pfister & DeMaster (2006)).

species	current estimate	historic estimate	area/population
beluga	19 784	19 784	eastern Bering Sea/Bristol Bay
Dall's porpoise	90 141	90 141	Bering Sea/Aleutian Islands
harbour porpoise	50 127	50 127	Bering Sea
harbour seal	35 688	170 000	Bering Sea/Gulf of Alaska
northern fur seal	888 120	3 000 000	eastern North Pacific/Bering Sea
sea otter	41 474	118 000	southwest Alaska
Stellar sea lion	35 194	126 900	western North America

(iv) the caloric values of these tissue types, and (v) the proportion of the carcass (or tissue type) that is consumed. Inherent in the last variable are limitations in meal size and processing rates of killer whales.

We will begin by determining how many transient killer whales could be sustained on various dietary scenarios involving only the great whales and end by asking whether or not the smaller marine mammals were sustainable in the face of killer whale predation following the decline of great whale food resources.

Because full demographic schedules (birth and death rates by age or age class) have not been accurately estimated for any large whale population, we instead relied on three commonly used summaries of life-history patterns that have been estimated for most great whales: age at maturity; 'natural' (non-anthropogenic) adult mortality rate; and inter-birth interval. As described in Doak *et al.* (2006), we used these rates to assemble a simple two-stage (juvenile and adult) demographic description for each of the major great whale species in
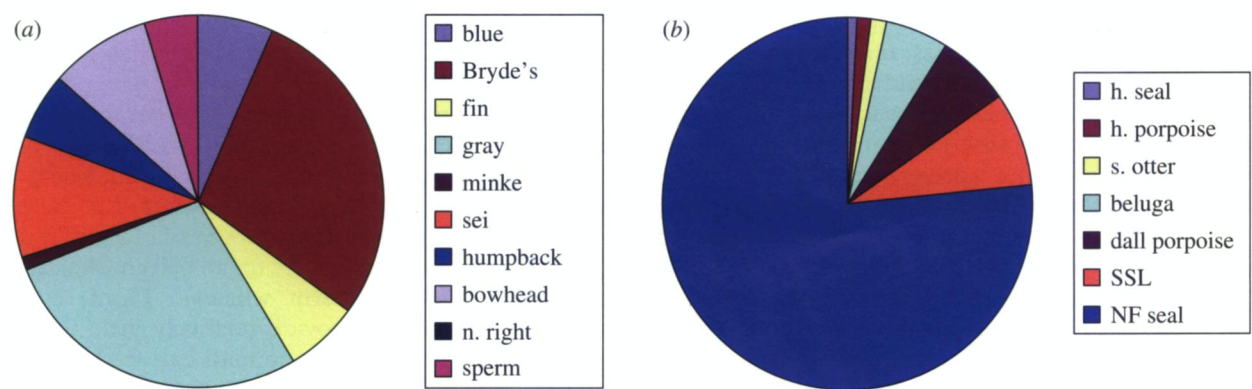
Figure 6. Fractions of food resources for killer whales estimated for each guild of prey under current population numbers. (*a*) Relative food resources presented by each great whale species under current population estimates and assuming that young, minkes, and tongues and blubber of adults consumed. (*b*) Relative food resources presented by each small marine mammal species under current conditions. (n, northern; h., harbour; s., sea; SSL, Stellar's sea lion; NF, north fur.)
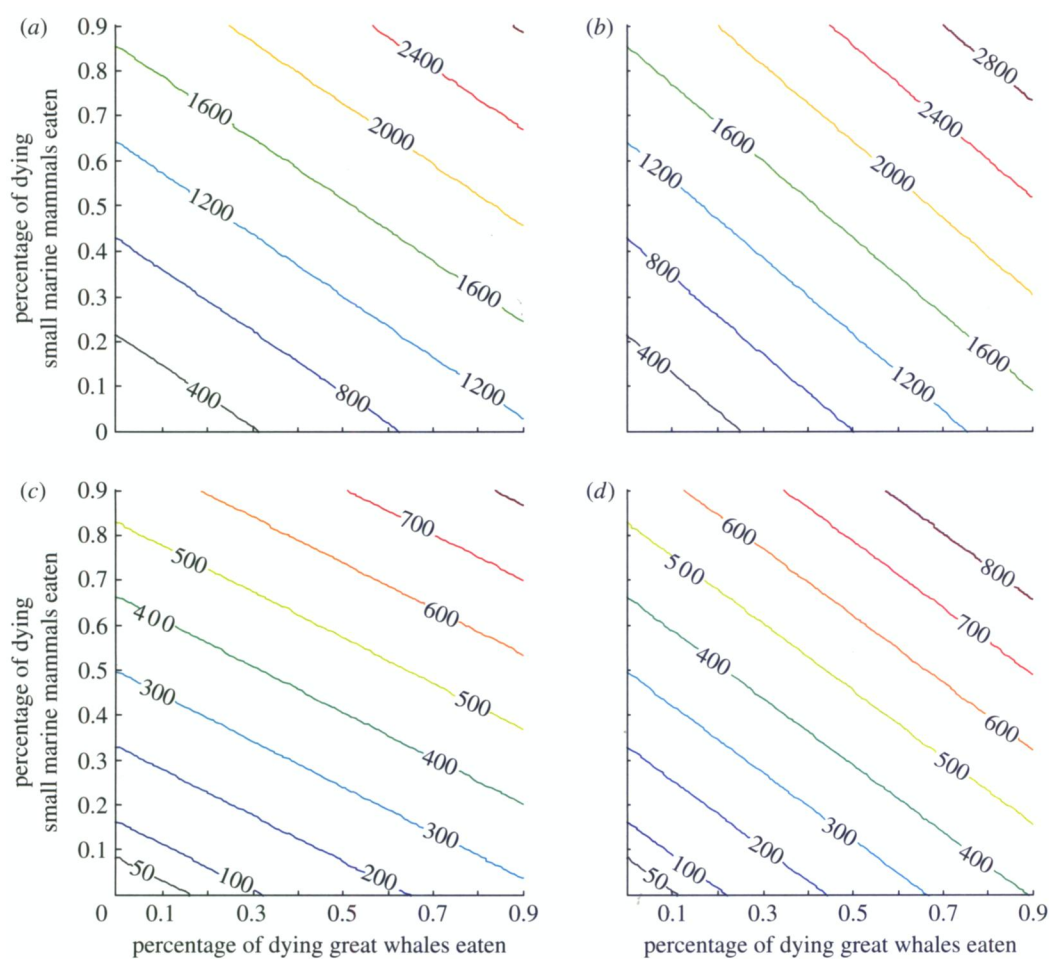

Figure 7. Isoclines indicating the number of transient killer whales supportable with different combinations of proportional prey consumption of great whales (*x*-axes) and small marine mammals (*y*-axes). (*a,b*) Results for historic population estimates of each prey are shown, and assuming either (*a*) limited or (*b*) broader consumptions of great whales. (*c,d*) Results for current population estimates of each prey are shown, and assuming either (*c*) limited or (*d*) broader consumptions of great whales. All results assume mean food resources over the range of parameter values governing population regulation and consumption patterns, as described in the text. Note that the current minimum estimate of transient killer whales in this area is 400.

the North Pacific: blue; Bryde's; fin; grey; minke; sei; humpback; bowhead; northern right; and sperm whales. These 10 species represent the majority of great whale numbers in the North Pacific now and in the past. In addition to the demographic rates, estimates of total mortalities rely on population estimates, which we obtained from Pfister & DeMaster (2006).

Seven species of small marine mammals are common in our region of interest: harbour seal; harbour porpoise; sea otter; beluga whale; northern fur seal; Steller sea lion; and Dall's porpoise. While several species of ice seals (spotted, ringed, ribbon and bearded), and the Pacific walrus, also approach our region, they are unlikely to be major food resources for

killer whales in the Aleutian region and we therefore do not include them in our analyses. For each of the other species, we created an age-dependent, two-sex demographic model. For the harbour seal, we could rely on the data from Pitcher (1990) for survival and growth estimates. For all other species, empirical data on demographic rates are partial and, for survival rates, often inconsistent. Therefore, we used the allometric relationships for survivorship in Trites & Pauly (1998) to approximate size-specific survival rates for each species and used information in various chapters of Perrin *et al.* (2002) to obtain reproductive rates. Along with the estimates of abundance (table 1, from Pfister & DeMaster 2006), these demographic schedules can provide both current and historical estimates of the production of dead animals.

While we used the basic demographic models just outlined to make production estimates from current numbers, predicting historical production rates requires an additional set of assumptions. Since marine mammal stocks were presumed to be more or less stable prior to industrial exploitation, demographic rates must have been different from those currently estimated. However, which rates differed and by how much is unknown. At one extreme, it is possible that fecundities were unaffected by reductions in numbers (see Mizroch & York 1984), but mortality rates were considerably higher than currently estimated. This pattern of density-dependent effects would yield the maximum production of dead animals for a stable population of a given size. Conversely, as the numbers increase survival might be unaffected, but fecundities lowered to achieve population stability. This would result in the minimum number of deaths for a given stable population size. Since both extremes and many mixed responses to density are known in mammals, we modified all our population models in two ways, by reducing only fecundity or reducing only survival. We then used these two types of models in conjunction with historical population estimates to arrive at an estimated numbers of deaths.

We next calculated the number of killer whales that could be supported from the sustainable number of great whale or small mammal deaths. We assume that adult male killer whales require 287 331 kcal d^{-1}, while females require approximately 193 211 kcal d^{-1} (these figures account for assimilation efficiency: Williams *et al.* 2004). For small marine mammals, we made the simple assumption that all of each carcass is consumed, and used a standard estimate of 2.5 kcal g^{-1} for all species. Thus, the conversion of a predated animal into food is quite simple.

For great whales, the situation is more complex, with the conversion of dying whales into killer whale food depending on several factors. First is the composition of the tissues actually consumed. Although detailed data on the caloric content of whale tissues are not available, we use information on both whale tissue and other mammals to estimate that whale tongues provide 2.07 kcal g^{-1}, a mixture of whale meat and blubber has approximately 2.5 kcal g^{-1} and blubber alone has approximately 4.0 kcal g^{-1} (Williams *et al.* 2004). Second, we need to specify which animals are predated commonly enough to be worth considering.

We considered two patterns, which reflect familiar ideas about the preferences of killer whales: (i) only juvenile whales (and adult minkes) are predated, and since a mixture of blubber and meat would be consumed, the average energy gain is 2.5 kcal g^{-1} and (ii) juveniles and minkes are consumed (2.5 kcal g^{-1}), as are tongues (2.07 kcal g^{-1}) and blubber (4.0 kcal g^{-1}) of adults, but only a limited amount of blubber is used (up to the mass of the tongues for all baleen whales, and up to 1000 kg for sperm whales). Third, even a predated whale may provide relatively little food for killer whales, if only a few animals can feed upon the carcass before it sinks. Owing to sinkage, in the different model runs we conservatively assume that each killer whale can feed either once or twice on a great whale kill, thus constraining maximum input per kill for each individual killer whale to 125 kg for adult females and 186 kg for males (estimated from the data provided by McBain, Sea World and the proportional metabolic needs of males and females). Documented group sizes of hunting killer whales range from 5 up to 35 (Reeves *et al.* 2006), so we ran the calculations with pack sizes of 10, 20 or 30 animals feeding at once on each prey individual.

Finally, for all prey species, we have no quantitative data on the fraction of dying animals that are predated. Because we have no good information on this for any prey species, we ran estimates of each group of prey (large whales versus small marine mammals) for predation-caused/scavenged deaths that range from 5 to 50 per cent. We summarize many of our analyses over this range to emphasize its key importance in driving our results.

7. RESULTS

With the different estimates of attack patterns and rates, and the resulting calories that could be gained by killer whales, we generated multiple estimates of the supportable numbers of killer whales. At current numbers and over the range of predation rates modelled, neither great whales alone (figure 5*a,b*) nor small marine mammals alone (figure 5*c*) can support large populations of killer whales. However, it is also important to note that the difference between historic and current population sizes of these prey groups generate large differences in supportable predators. In presenting these results, we primarily seek to show that even very selective and low rates of predation would still allow a substantial population of killer whales to subsist on great whale stocks, especially before their depletion. Not surprisingly, if large fractions of prey are consumed, either prey group can support populations of killer whales numbering in the hundreds.

One key point to make is that in our analyses we have—given no useful data to do better—caused the percentage of each species with each prey group to be predated at the same rate. What this means is that the more abundant prey species are most critical in determining the number of supportable killer whales (figure 6).

For the interpretation of our results, the current abundance of transient killer whales is a key variable.

We use the current photo identification record of approximately 400 individuals (NOAA, http://www.afsc.noaa.gov/nmml/cetacean/research/killer.php), recognizing that the number is not less than this but could be substantially larger. We also assume this number has not increased over the past five decades. With this as a minimum predator population that must be sustained by some food source, we can then re-examine our results. Most critically, in the modern system, it appears to be impossible for small prey populations to sustain the transient killer whales unless the cause of death is greater than 50 per cent predation for all these species (figure 5c). Similarly, current great whale populations do not appear to be, alone, capable of supporting 400 killer whales, unless some of our more conservative assumptions about consumption patterns are incorrect.

We next combined the analyses of both prey groups to ask what combination of predation rates (in the sense of fraction of dying animals that are fed upon) could sustain what sizes of mammal-eating killer whale populations. The results suggest that historically quite low predation rates, 0.35 or less, of either or both groups would be sufficient to support approximately 400 predators (figure 7a,b). However, under current conditions, only quite substantial predation rates on *both* groups appear capable of providing the prey base needed by 400 killer whales. Even if 50 per cent of all small marine mammals are killer whale food, between 20 and 40 per cent of great whale deaths would be needed to sustain 400 predators. While we obviously do not maintain that these exact numbers are correct, the results suggest that understanding what combination of food resources maintain transient killer whales is a real problem, and also that the rates of predation on different prey species needed to support these predators must be high enough that anthropogenic changes in their food resources are nearly certain to have propagating effects within this community.

8. DISCUSSION AND CONCLUSIONS

Several important points are evident from these analyses. First, the production potential of great whales and small marine mammals are roughly equivalent if we assume that the small marine mammals are consumed in their entirety while only a single meal is taken from a large whale kill. If large numbers of transient killer whales are attracted to and feed on large whale kills (as has been observed—Pitman *et al.* 2001); if killer whales cache large whale carcasses in order to obtain multiple meals from them, as they apparently do (C. Matkin 2008, personal communication); if there is surplus killing, or if some animals escape attacks but are wounded and later die, as apparently sometimes occurs (Sheldon *et al.* 2003); or if some small marine mammals are only partially consumed, as occurs with small cetaceans such as belugas (Vos & Shelden 2005) and Dall's porpoise (R. Brewer 2008, personal communication), then larger proportions of the total mortalities would have to go into fuelling killer whales to sustain the system. Second, whaling strongly influenced the estimated points of proportional sustainability. Before whaling, the entire present-day

transient killer whale population could have sustained itself by taking a single meal from some 20–40% of the great whale deaths, depending on the exact scenario (see above). Great whales today are incapable of sustaining transient killer whales, unless adults and calves of all species are being eaten (figure 5). Third, approximately 30 per cent of all marine mammal deaths would have to be consumed by transient killer whales to achieve sustainability in the present-day system. By themselves, approximately 60 per cent of the total small marine mammal deaths would have to be consumed to achieve sustainability. This seems rather high based on comparable measures from other large predator–large prey systems. Fourth, all of these conclusions are sensitive to minimizing assumptions. If the population of transient killer whales is much larger than the 400 or so individuals known from photo identification, small marine mammals by themselves could not sustain these predators under any calculable circumstance. Even more importantly, each of our specific analyses is based on the assumption that all prey species are being consumed simultaneously as a common, maximum sustainable resource. If there is any species selectivity in transient killer whale foraging in space or time, the likelihood of small marine mammal population persistence as a killer whale prey resource would probably be much diminished, especially in the absence of great whale food subsidies.

Although our inferences concerning the sustainability of interactions between killer whales and their marine mammal prey are based entirely on models and simplifying assumptions, it is important to keep in mind the conservative nature of our most important metric—the prey requirements of killer whales. As pointed out above, the estimate of transient killer whale abundance is an empirically derived minimal value. If the population of transients is larger than this, the array of sustainable scenarios becomes even fewer and more demanding of multiple prey. Likewise, the estimate of field metabolic rate employed in our demographic/energetic model is a stripped-down conservative value. Lactation, pregnancy and growth, the likelihood that lean meat as opposed to blubber is often consumed and the differential activity costs will all act to increase energetic requirements, which again would act to decrease the array of sustainable scenarios. For some of these—activity and lactation being two of the most important—the impact on energetic costs can be four- to sixfold higher than our estimates (e.g. Williams *et al.* 2007).

More generally, our descriptions and analyses of marine food webs in southwest Alaska provide evidence for a diversity of important linkages and interactions involving large vertebrates. The recent collapse of sea otter populations has resulted in a wholesale reorganization of the kelp forest ecosystem, with effects extending to multiple species from the bottom to the top of the food web. Although more speculative, similarly strong food-web interactions involving large vertebrates appear to have occurred in the oceanic ecosystem, even acting in such a manner as to link with the coastal systems through a predator–prey relationship between killer whales and sea otters. By perturbing these

predator–prey assemblages, the potential has been established for population oscillations and alternative stable states. Both seem likely, the more so because of the longevity of the predators involved and the relatively slow rate of marine mammal population increase. The loss of sea otters clearly drove the coastal ecosystem to an alternative phase state, a shift that may also be characterized by hysteresis (Sheffer *et al.* 2001). The depletion of large whales may have set in motion an ecological chain reaction of such profound strength and complexity that reversibility might take decades or may even no longer be possible.

There can be little doubt that marine mammals are central players in the dynamics of higher latitude marine food webs. This conclusion is reinforced by growing evidence for key ecological roles of large vertebrates in other ecosystems, including wolves, grizzly bears and cougars in North America (McLaren & Peterson 1994; Berger *et al.* 2001; Ripple *et al.* 2001), large felids and birds of prey in the New World tropics (Terborgh *et al.* 2001), sharks in coastal marine systems (Myers *et al.* 2007) and large predators in Africa (Sinclair *et al.* 2003; Owen-Smith & Mills 2008). The implications for conservation are profound. Strategic habitat management is necessary but insufficient for the maintenance of biodiversity. Biodiversity conservation, in addition, requires the maintenance or restoration of food-web interactions involving large vertebrates.

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